The process whereby theory motivates experiments and experiments guide theory is central to the emerging field of computational neuroscience. The present experiments, for example, were motivated in part by theoretical proposals, but those proposals now require substantial revision to become compatible with our findings. This cycle will surely continue because the algorithms implemented by the brain are likely to be far more complex and sophisticated than anything yet conceived by experimentalists or theorists.

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- 11. Recordings were made from four macaque monkeys (Macaque nemestrina) anesthetized with Sufentanil (5 to 12  $\mu$ g per kilogram of body weight per hour, intravenously). Appropriate anesthesia doses were determined for each animal before paralysis. During Flaxedil-induced paralysis (7 to 15 μg kg<sup>-1</sup> body weight hour<sup>-1</sup>, intravenoùsly) anesthesia was monitored and adjusted according to standard criteria for electrocardiographic and electroencephalographic responses, including the absence of responses to noxious stimuli. Single-unit recordings were made with Levicktype electrodes inserted into the prelunate gyrus and lunate sulcus through a customized recording chamber. Additional details concerning recording and surgical procedures are given by D. J. Felleman and D. C. Van Essen [J. Neurophys. 57, 889 (1987)] and by J. F. Olavarria, E. A. DeYoe, J. J. Knierim, J. F. Fox, and D. C. Van Essen [ibid. 68, 164 (1992)]
- 12. The receptive field of each isolated unit was determined with a computerized visual stimulator. The stimuli were shown in the optimal color for each cell as determined in a preliminary test. They were displayed for 0.5 s on a gray background with a luminance that was roughly equal to the mean luminance of the stimuli ( $\sim$ 10 candela m<sup>-2</sup>). The stimuli covered the estimated receptive field and spanned a range of spatial frequencies surrounding the preferred frequency of a cell. Two or three phases were tested. Cartesian sinusoidal gratings were mixed with non-Cartesian gratings to facilitate comparisons of response rates. The partially randomized stimulus sequence was shown between three and eight times as needed to achieve consistent estimates of response magnitudes.
- Cells were classified by comparison of the response rate obtained with the optimal Cartesian

## M TECHNICAL COMMENT

# Tritium and Radiocarbon Dating of Canada Basin Deep Waters

 $\mathbf{T}$ wo of us (R.W.M. and E.C.C.) recently applied radiocarbon data to determine the rates of nitrate (NO3-) regeneration and oxygen  $(O_2)$  depletion in the Canada Basin of the Arctic Ocean (1). A one-dimensional, time-dependent diffusion model was used to calibrate the age of the deep water. The combination of this model with a model of an organic carbon (C) flux (2), suggested (1) how C fluxes into the basin might reflect primary productivity within the central Arctic Ocean. We wish to correct an error in the age estimates of the basin water (1) and to suggest where the basin-derived estimate of C flux might fit into the larger scheme of primary production in the Arctic Ocean.

The bottom waters of the Canada Basin

are old and appear not to be affected by recent inputs from dense waters produced on the shelves (1, 3, 4). This point is central to the assumption of a stagnant basin that undergoes property exchange only by top-down diffusion or by particle flux. However, as seen in table 1 of (1), detectable quantities of tritium have penetrated the top of the basin. While not contradicting the proposed model, the tritium data imply that radiocarbon from bomb tests has also penetrated the top of the basin, and this must be accounted for before radiocarbon ages can be used to calibrate the model. For the Arctic Ocean, tritium and <sup>14</sup>C data (3, 5) suggest an appropriate correction to be 3.5 per mil in  $\Delta^{14}$ C for each 0.1 tritium unit (TU) above the "pre-

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grating to that obtained with the optimal non-Cartesian grating. Response distributions were normalized and were then compared with a t test. Because there were more Cartesian than non-Cartesian gratings in the stimulus set, this is a conservative test with a bias against classification of cells as non-Cartesian.

- In our preliminary recordings from area V2, we found a few cells (2 of 22 tested) that showed a significant preference for non-Cartesian gratings.
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- 16. Additional evidence against size selectivity as a cause of non-Cartesian stimulus preferences comes from our anecdotal observation that many non-Cartesian cells responded only weakly to the bars of variable size and orientation used in our manual receptive field plotting procedure. Also, in the preliminary results of a test that systematically varied the width and length of Cartesian gratings, size selectivity failed to account for the response characteristics of 14 of 20 cells initially classified as non-Cartesian.
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bomb value" [assumed to be about 0.10 TU (6)]. We have rerun the model, making this correction and choosing -55 per mil for the value of the prebomb <sup>14</sup>C concentration (3, 6). The new calculation yields an effective deep water age of about 500 years, not 983 years as estimated in (1); the new vertical diffusion coefficient is about 3.9 ×  $10^{-5}$  m<sup>2</sup> s<sup>-1</sup> [the estimate in (1) was 2.3 ×  $10^{-5}$  m<sup>2</sup> s<sup>-1</sup>].

The new calculations, which reduce the deep water age by about a factor of 2 and increase the vertical diffusion, show that larger fluxes are required to reproduce the NO<sub>3</sub><sup>-</sup> and O<sub>2</sub> profiles than was assumed in (1). Thus, for the 1500-m boundary, we estimate the NO<sub>3</sub><sup>-</sup> flux to be 5.9 mmol m<sup>-2</sup> year<sup>-1</sup>, the O<sub>2</sub> utilization rate to be 63 mmol m<sup>-2</sup> year<sup>-1</sup>, and the respective C fluxes to be 0.47 to 0.58 g m<sup>-2</sup> year<sup>-1</sup>. For the deep Atlantic Ocean, W. S. Broecker *et al.* (6) correlated the change ( $\Delta$ ) in <sup>14</sup>C with  $\Delta$ O<sub>2</sub> content and arrived at a slope of 0.8 mmol m<sup>-3</sup> O<sub>2</sub> per mil  $\Delta$ <sup>14</sup>C. As radiocarbon decays at 10 per mil per 80 years, Broecker *et al.* (6) the mean O<sub>2</sub> utilization rate was 10 mmol m<sup>-3</sup> per

century. We find for our data a slope of 0.32 mmol m<sup>-3</sup> O<sub>2</sub> per mil (r = 0.85, n = 8) and 0.023 mmol m<sup>-3</sup> NO<sub>3</sub><sup>-</sup> per mil (r = 0.75, n = 8). These slopes yield O<sub>2</sub> utilization rates of 4 mmol m<sup>-3</sup> per century (based on O<sub>2</sub>) and 2.6 mmol m<sup>-3</sup> per century (based on NO<sub>3</sub><sup>-</sup>). It should be noted that these linear correlations do not explicitly account for hypsometry or variation of rates with depth. Nevertheless, this comparison implies that O<sub>2</sub> utilization rates in the deep Atlantic.

The use of deep fluxes of C to estimate primary production at the surface is a tenuous method (7). Nevertheless, several models do so because the mechanics and rate of C transfer in the sea is important in climate models and to deep ocean biogeochemistry. When we used "Suess or Berger relationships" (7), as in (1), our calculations of carbon fluxes at 1500 m implied a total surface primary productivity of 20 to 30 g C m<sup>-2</sup> year <sup>-1</sup>. With the use of the relation proposed by W. Berger (8) to link new production (NP) with the estimated total production (PP)  $[NP = (PP)^2/410]$ , we arrived at a figure for new production of about 1 to 2 g C m<sup>-2</sup> year<sup>-1</sup>. According to these calculations, the flux across the 1500-m boundary is about 25 to 50% of the NP, which seems very high. This calls into question the general applicability of the models which, it may fairly be argued, are here being applied beyond the data base used to construct them. Direct measurements of vertical flux in the Canada Basin will be required to resolve whether or not flux models such as those listed by J. K. B.

Bishop (7) are appropriate to the Arctic.

In (1), different estimates of PP were compared to one that was obtained with the use of a model [figure 3 in (1)] in which the deep water of the basin behaves like a sediment trap collecting the vertical rain of C fixed at the surface, which reflects primary production only for the deep basin. However, the Arctic has large shelves (35% by area) that may export regenerated products into the Arctic interior halocline (9). Hence, primary production estimates that are based on dissolved properties of the halocline (9, 10) are not directly comparable to values of primary production obtained here, because the former reflect cumulative contributions from the shelf and interior domains. Also, it is unknown how much particulate matter is exported from the shelf to settle in the deep basin.

There has been a continuing debate about how much shelf-produced C is exported to ocean interiors. Nowhere is this process likely to be more important than in the Arctic. Broecker *et al.* (6) note that "Getting the deep Atlantic right is proving to be a difficult task." The Arctic Ocean is proving even more difficult, because there are two major basins that appear to be oceanographically separated from one another. Transects of high quality have only recently been acquired for the Eurasian Basin (11); the Canada Basin remains the last major basin for which there is no transect.

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